

Sexual Characteristics of *Margaritifera margaritifera* (Linnaeus) Populations in Central New England

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(1 Text figure)

INTRODUCTION

BIVALVE MOLLUSKS are considered to be characteristically dioecious (gonochoristic) (COE, 1943). The few instances of consecutive or simultaneous hermaphroditism are believed to be chiefly confined to species in which larval or developing young are brooded in the gills or demibranchs of the parent (FRETTER & GRAHAM, 1964). Furthermore, it is generally found that species which are hermaphroditic are typically found in harsh or fluctuating environments. Both of the above conditions are characteristic of fresh water and tidal habitats.

Hermaphroditism has been explored in the Holarctic fresh water Unionacea by a few investigators (BLOOMER, 1934; TEPE, 1943; HEARD, 1970, 1975; VAN DER SCHALIE, several papers, summarized in 1970). These studies showed that fully hermaphroditic species were rare, although many species contained an occasional hermaphrodite. Populations of the Margaritiferidae, the most remote group morphologically within the Unionacea (ORTMANN, 1911; HEARD & GUCKERT, 1970), have been examined in Europe and North America. Studies by HENDLEBERG (1960) and VAN DER SCHALIE (1966, 1970), complete with summaries of earlier investigations, have indicated that *Margaritifera margaritifera sensu lato* is normally dioecious with only an occasional hermaphrodite being evident.

HEARD (1970) examined specimens of *Margaritifera falcata* (Gould, 1850) occurring in North American Pacific drainages. Finding all his material hermaphroditic, he concluded that *M. "falcata"* was hermaphroditic, thus proving an exception to the supposition of uniform unisexuality among the Margaritiferidae. However, VAN DER SCHALIE (1970) listed the locality of his own (1966) *M.*

margaritifera material (cited by HEARD, 1970) as occurring in the Snake River watershed in Wyoming. The Snake River drains the Pacific side of the Continental Divide and the *Margaritifera* inhabiting these waters is *M. m. falcata* (= *M. "falcata"*) (Henderson, 1935). Each study was on a single population sampled on a specific date. Assuming that van der Schalie's material was "*falcata*," it is uncertain whether *M. "falcata"* as a whole, is distinctly hermaphroditic, or dioecious with occasional hermaphroditism, although BURCH (1973) used hermaphroditism as a criterion distinguishing *M. "falcata"* from *M. margaritifera*.

The present study analyzes several populations of *Margaritifera margaritifera* inhabiting the Connecticut River system in central New England. Histological examination of the gonads was performed to determine sexual characteristics of these populations. Individuals of all ages collected at different times of the year were sectioned. Special attention has been paid to the distribution of sexes with respect to age, and to the possibility of sex reversal(s).

METHODS AND MATERIALS

A total of 52 specimens was utilized for visceral histological examination. All specimens were fixed in 10% formalin and preserved in 70% isopropyl alcohol.

The collections represent 13 populations occurring within the Connecticut River watershed in Massachusetts. A randomly collected sample, (MO. 896) Munn Brook, Westfield, Hampden County, of 18 specimens was used for sex ratio determination. All preserved material relevant to this study is maintained in the invertebrate collections of the Museum of Zoology, University of Massachusetts at Amherst.

Three specimens from a single locality (MO. 683) were selected for exploratory sectioning of gonads. All removed portions were embedded in paraffin and serially sectioned at $8\mu\text{m}$. Sections were then dehydrated in alcohol, cleared in xylene, stained and mounted with Pycolite. The serial sections were stained principally with Harris' hematoxylin and counterstained with eosin. Some material was stained with Ehrlich's hematoxylin. Fast green and acid fuchsin were also occasionally used as counterstains.

All parts of the gonad of each animal were removed and sectioned for examination for possible hermaphroditism. At least 25 slides, each consisting of about 4 sections, were prepared for each individual. This method was specifically employed in order to reveal rare tissues of an opposite sex in the same gonad, assuming that all animals were normally hermaphroditic. This criterion is based on HEARD's (1970) statement that, although *Margaritifera falcata* was normally hermaphroditic, male gonadal tissues were fewer than female.

At least 10 slides per animal were prepared for the remaining material except MO. 896 (18 specimens) and 7 follow-up specimens for which 5 slides per animal were prepared.

Ages of mussels 10 years and younger were determined by counting shell annuli, while older specimens' ages were determined by the application of growth curves developed previously for age analysis of Connecticut River system populations (SMITH, 1976).

RESULTS AND DISCUSSION

Histological analysis of the gonadal tissue of investigated mussels show that *Margaritifera margaritifera* in central New England is dioecious. Not a single case of hermaphroditism was disclosed. Inspection of gonads removed from specimens collected at different time intervals during the growing season (spring-fall), and including the recruitment period, did not reveal any follicular units undergoing sexual transformation, suggesting that individuals remain in a specific sex state during the warm season. It is not evident, however, whether an animal can undergo sex reversal at other times of the year nor if animals engage in sex changes at some particular period during their lifespan.

All inspected adult animals participated in the late summer - fall recruitment. Normal gametogenesis was observed from mid-May to early August after which spawning commences (SMITH, 1976). Sperm morulae, as

described and discussed by VAN DER SCHALIE & LOCKE (1941) and HEARD (1969, 1975) for other freshwater mussel species, were present in male follicles during June. By July all sperm morulae had disappeared and the acini were fully charged with mature sperm. Mature ova in females began appearing by mid-June and all acini contained fully mature ova during July. The histological evidence available during the spawning period indicates that females deposit eggs into the demibranchs prior to the release of sperm by males, suggesting that fertilization occurs after the eggs are in the demibranch marsupia. Following deposition of eggs, a few mature and immature oocytes remain in the ovary, however; these are apparently resorbed after a few weeks.

Identifiable sex cells are seen in animals between 7 and 9 years of age, whereas sexual maturity, as indicated by the ability to produce mature gametes, is not achieved for another year or so. The differences in time to reach sexual maturity appeared to be sex-dependent in examined mussels. Males apparently mature 1 to 2 years earlier than females (Figure 1). A female probably does not function reproductively until its 9th year, which is halfway through its normal lifespan of 19 to 25 years estimated by SMITH (1976) for populations in central New England.

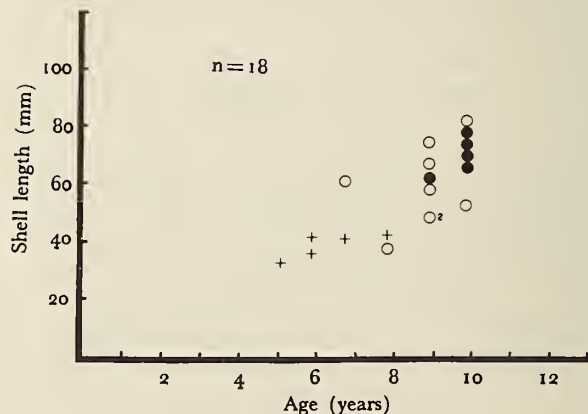


Figure 1

Distribution of juvenile and young adult specimens
 + - sex cells are unrecognizable ○ - males ● - females

Sexual maturity is gradual, as succeeding older mussels show greater amounts of gonadal tissue per unit area

of viscera. After mussels have become fully functional reproductives the correlation between the dominance of a particular sex and individual age disappears. Mature mussels of each sex are nearly equally distributed. Analysis of the Munn Brook population shows a moderate (5:3 or 23%) preponderance of females over males in the 9 to 15 year age category. This ratio slightly exceeds that given by PELSENEER (1926) for several unrelated molluscan forms he studied. However, the dominance of females over males is in agreement with his observations. The available information does not indicate any protandric tendencies, although a slight male over female dominance existing in the pre-9 year old classes is replaced by a female over male dominance later on. Males are present in the older age classes of the Munn Brook population and among other examined specimens from many populations, large older males (> 100mm shell length) are abundant.

The reasons for early male dominance followed by female dominance later on can not be explained by the available evidence and deserves further study. However, the appearance of males before females has been demonstrated for rhythmic and protandric hermaphroditic mollusks (COE, 1936). Early male preponderance has been suggested to be the result of bioenergetic economics wherein it is functionally easier or more economical to be male than female (RUSSELL-HUNTER & McMAHON, 1976).

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